

Thermal ecology of the Pygmy Alligator Lizard, *Gerrhonotus* parvus Knight and Scudday, 1985 (Squamata: Anguidae), in Nuevo Léon, Mexico

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Introduction

Temperature is one of the most important abiotic factors that affect organisms (Allee and Park 1939; Sinervo et al. 2010), and is perhaps the most acute of all (Angilletta et al. 2002; Huey et al. 2010) because it affects all aspects of their physiological performance (Hutchison and Dupré 1992). It can influence the distribution and ecology of lizards since certain species regulate their body temperature within a relatively narrow range during their activities that corresponds to the optimum for their metabolism, locomotion, and other physiological functions (Angilletta et al. 2002; Bowker and Johnson 1980). These organisms control their body temperature by a combination of both behavioral and physiological patterns (Bowker 1984; Hertz et al. 1982; Huey 1982). Thus, the impacts of changes in the

environmental temperature on populations depend on the acclimatization, thermoregulatory behavior, habitat selection, and changes in the patterns of daily activity, in addition to changes in phenology and reproduction (Deutsch et al. 2008; Huey and Slatkin 1976; Huey et al. 2009; Kearney et al. 2009), and perhaps, ultimately, by their ability to follow changes in the thermal niche (Lara et al. 2015). Therefore, the study of thermal ecology has become integral to our understanding of the ecophysiology of these reptiles (Angilletta 2009; Avery 1982; Bartholomew 1982; Sinervo et al. 2010).

Thermoregulatory strategies among reptiles range on a continuum from thermoconformity to active thermoregulation (Huey and Slatkin 1976). Some lizard species are predominantly thermoconformers; so, for example, they keep their body temperatures similar to those of the environment (Hertz et al. 1993; Piantoni

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et al. 2016; Ruibal 1961; Rummery et al. 1994). Others are accurate thermoregulators which can maintain temperatures close to their preferred body temperature and above the ambient temperature (Bauwens et al. 1996; Christian 1998; Gutiérrez et al. 2010; Ibargüengoytía et al. 2010; Lara et al. 2015; Sartorius et al. 2002; Valdecanto et al. 2013). Genera such as Anolis and Liolaemus present intrageneric variation in their thermoregulatory strategies, with some species being thermoregulators and others thermoconformers (Piantoni et al. 2016). Thus, observations have indicated that a spatial distribution pattern for thermoregulation exists, such that close to the equator and at low elevations, the incidence of thermoconformity increases, leading to a limited capacity for adapting to climate change (Huey et al. 2003; Sears et al. 2011). On the other hand, Gerrhonotus species tend to have a fragmented distribution with low abundance, so that more information on the thermal ecophysiology of these populations is urgently required. Such information will allow a better understanding of the thermoregulatory strategies that are present in various populations which occupy different habitats and during different seasons of the year, and an understanding of these strategies can assist in the conservation of potentially vulnerable populations. For this reason, the objective of the present study is to analyze the basic thermal ecology of Gerrhonotus parvus in northeastern Mexico.

The genus Gerrhonotus is represented in Mexico by eight species: G. farri, G. infernalis, G. lazcanoi, G. liocephalus, G. lugoi, G. mccoyi, G. ophiurus, and G. parvus. Of these, the most widely distributed are G. liocephalus in western and southern Mexico and G. infernalis in central and northern Mexico and southern Texas (Good 1994). The remaining species are found in small areas and are known from only a few individuals. Gerrhonotus ophiurus is distributed in Tamaulipas, Nuevo León, central and southwestern San Luis Potosí, eastern Querétaro, Hidalgo, Tlaxcala, Puebla, and the mountainous areas of northern Veracruz (Lemos-Espinal and Dixon 2013; Nevarez de los Reyes et al. 2019); historical G. lugoi was isolated in the Basin of Cuatrociénegas, Coahuila (McCoy 1970), but recently it has been reported in Nuevo León (García-Vázquez et al. 2016; Montoya-Ferrer et al. 2021); G. farri is found near Tula, Tamaulipas (Bryson and Graham 2010); G. mccoyi is known only from the shores of several small lagoons, and in the Basin of Cuatrociénegas, Coahuila (García-Vázquez et al. 2018); and G. parvus is known only from four localities in Nuevo León and one in Coahuila. In Nuevo León, it inhabits the municipalities of Galeana, Los Rayones, Santiago, and Santa Catarina (Banda-Leal et al. 2013, 2014b).

The four previously-mentioned small species (*G. farri*, *G. lazcanoi*, *G. lugoi*, and *G. parvus*) have restricted distributions and very little is known about their biology. For *G. farri* and *G. lazcanoi*, only the collecting data for a single specimen of each are known (Banda-Leal et al. 2016, 2017); and for *G. lugoi*, there is only a report

of reproduction in captivity that describes the courtship behavior and litter size (Lazcano et al. 1993). For G. parvus, some details are available about its natural history based on work that began when it was first described in 1985 (Knight and Scudday 1985; Banda-Leal et al. 2002, 2005, 2013, 2014a,b; Bryson et al. 2003; Conroy et al. 2005; Banda-Leal 2016). In a recent document, Garcia-Vasquez et al. (2016) mentioned finding G. parvus in the municipality of Mina, Nuevo León. Although efforts have been made to understand the phylogenetic relationships of the species in this genus (Good 1988, 1994; Conroy et al. 2005), they remain unclear. The Pygmy Alligator Lizard, Gerrhonotus parvus, is an Endangered species known only from the Sierra Madre Oriental in the states of Nuevo León and Coahuila, Mexico (Fig. 1). Even though our group has written many articles on this species during the past decade, and much of this information was documented by Banda-Leal (2016), much still remains to be discovered in our understanding of the biology of G. parvus.

The characteristics of the few localities where G. parvus has been found can provide some insights regarding its habitat environments. The type locality of G. parvus is in a transition zone between pine forest (*Pinus arizonica*) and open gypsophyllous scrub, in a locality called Ejido de Santa Rita. This locality is a flat portion of the ejido (a communal piece of land), with patches of Texas Mountain Laurel (Sophora secundiflora), dispersed individuals of St. Peter's Palm (Yucca filifera), and some herbaceous plants, such as grasses and globular cacti (Coryphantha sp., Turbinicarpus beguinii, and Mammillaria sp.). There are some low hillsides with steep slopes, as well as canyons formed by streams, where limestone and chalky soils are present. On these slopes, piedmont scrub and rosetophilous scrub vegetation is found, and the pine community is composed of Arizona Pine (*Pinus arizonica*) and Mexican Pinyon Pine (*Pinus cembroides*). The elevational gradient in this area is 1,650–1,850 m.

However, the nature of the microhabitats at the other G. parvus localities suggest that it has a preference for dry limestone canyons. The second locality for the species is Cañon San Isidro, Santiago, Nuevo León. This canyon lies at an elevation of 1,600–1,750 m, runs east to west, is characterized by steep limestone walls covered with agaves (Agave sp.), sotols (Dasylirion sp.), and scrub oaks (Quercus sp.), and has intermittent pools of water. The canyon bottom has piles of leaf litter with scattered large rocks (Banda-Leal et al. 2002; Bryson and Lazcano 2005) where the specimens have been found. The third locality of Cañon Mireles, Los Rayones, Nuevo León, consists of piedmont scrub elements with a habitat similar to that of Cañon San Isidro, but with an elevation of 900 m (Conroy et al. 2005). The fourth locality is Cañon Reflexiones in the municipality of Santa Catarina, Nuevo León. This narrow canyon has an elevation of 1,650 m and is composed of limestone rock, with the presence of rosetophilous and piedmont scrub elements. An extensive list of the species found here was documented by Banda-Leal et al. (2014b).

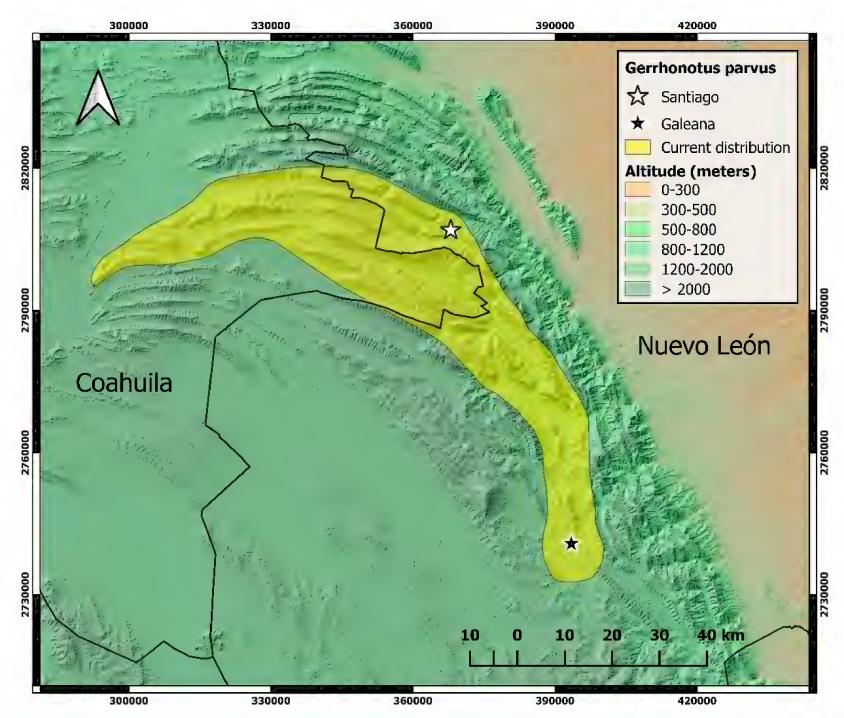


Fig. 1. Distribution of *Gerrhonotus parvus* in northeastern Mexico. The stars indicate the localities of specimens used in this study: Cañon de San Isidro, Santiago (white star) and Ejido Santa Rita, Galeana (black star). The coordinates are shown around the edges of the map in the UTM/WGS84 metric system.

The most recent findings of the species outside of Nuevo León were in the municipalities of Arteaga and Saltillo in the state of Coahuila in a Natural Protected Area called Sierra de Zapalinamé. Here, it was found at elevations from 1,700–3,100 m, with the vegetation types including desert scrub, submontane grasslands, gallery oak, and pine forests, depending on the specific localities where the specimens were found within the protected area. For example, the locality of Cañón de San Lorenzo, where most of the G. parvus were found, has one of the most diverse floral communities in the Sierra Madre Oriental. The dominant plant species are Sotols (Dasylirion cedrosanum), Chaparro Oak (Quercus pringlei), Little Bird Tree (Lindleya mespiloides), and Evergreen Sumac (*Rhus virens*) growing on a rocky substrate with abundant crevices. In the locality of the Paraje Aguajes area, the principal vegetation is composed mainly of Chaparro Oak, Mexican Drooping Juniper (Juniperus flaccid), Sotols, Lechuguilla Agave (Agave lechuguilla), and Apak Palm (Brahea dulcis). The other locality within the protected area is called Cerro de las Nieves II, where the main plant elements are Sotols, Chaparro Oak, Little Bird Tree, and various grasses (Banda-Leal et al. 2018).

The goal of this study was to gather more information about the thermal ecology of *G. parvus* in its natural

habitats. Three years of field surveys were conducted to locate specimens and obtain thermal measurements of the lizards themselves, along with data on the air and substrate temperatures where they were found.

Materials and Methods

Field surveys were conducted from 2012 to 2015 during the months of March–October. The previously known localities for *G. parvus* within the Sierra Madre Oriental in Nuevo León were surveyed. These localities were visited from 0800–1600 h at Ejido Santa Rita, Galeana, 4.5 km south of the entrance to the town of Galeana, in the Cañon de Mireles, and Los Rayones, 2.20 km to the northeast of the municipality capital of the same name, then in Cañon de San Isidro, Santiago. Two additional areas in which this lizard might potentially occur were also surveyed, i.e., Cañon de Reflexiones, Santa Catarina, 3.6 km south of the locality of Casa Blanca and the area in the foothills of Sierra Madre Oriental, 4.73 km east of Casa Blanca, Garcia, Nuevo León. A total effort of 1,400 person-hours was expended during these surveys.

The samples were assembled using the Campbell and Christman (1982) and Dodd (2016) methods, which consist of locating and capturing specimens on the

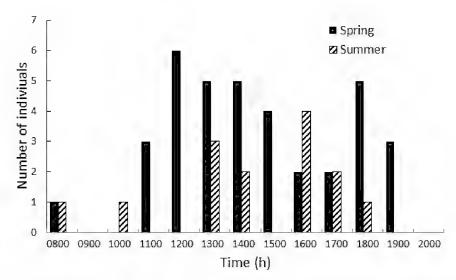


Fig. 2. Seasonal pattern of daily activity of *Gerrhonotus parvus* in Sierra Madre Oriental.

different substrates present, either under or on rocks, leaf litter, vegetation, and soil. The substrates were manipulated using hybrid herpetological hooks that are used for handling snakes (Professional Field Hook 45), herpetological forceps (Tweezers 24), and a borescope of 90 cm long (Extech BR200). The habitat structure used by the species in each locality was characterized and quantified according to the Brau-Blanquet method, which consists of establishing the percentages of the different structures that typify the habitat, such as rocky areas, leaf litter, vegetation, and soil (Kent and Coker 1992; Greenberg et al. 1994; Jellinek et al. 2004).

Each specimen was captured manually or with herpetological tweezers. Data recorded included the date, hour, and the body temperature (T_b) during the first 10 sec after capture, which was recorded with a thermometer Raytek (MiniTEMP) with a sensor sensitive to \pm 0.1 °C at 5 cm from the dorsal surface. The air temperature (T_a) was measured in the shade at 5 cm above the substrate where the individual was first observed, and the substrate temperature (T_s) was measured in the shade by touching the substrate where the individual was first seen. Also recorded were the SVL (mm), sex, the activity of the specimen, and location coordinates using the UTM, WGS84 (Garmin Etrex 10) metric system.

Simple linear regression was used to analyze the relationships of T_b with T_s and T_a . To determine whether this species is a thermoregulator or thermoconformer, the criteria used by Huey and Slatkin (1976) were applied. According to these criteria, a species is a thermoregulator when the slope of the linear regression of the T_h and the environmental temperature (T_a or T_s) is zero or close to zero, and a species is a thermoconformer when the slope is one or close to one. In addition, if the correlation between T_b and T_a is greater than the correlation between T_b and T_s , then the organism is assumed to have a heliothermic tendency; while the tendency is thought to be thigmothermic if the opposite correlation is found. Significant differences between T_b and either T_s or T_a were tested using an Analysis of Variance (ANOVA), and the significance value used for all statistical tests was P <0.05. Post-hoc pair-wise comparisons (Tukey Test) were tested for significance. The tables and results in the text

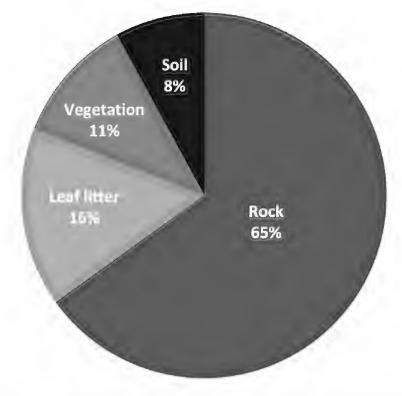


Fig. 3. Proportions of microhabitats used by *Gerrhonotus* parvus.

show the average \pm standard error, sample size (N), and temperature range (Sokal and Rohlf 2000).

Results

General Observations of the Specimens Found, Their Behaviors, and Habitats

During the course of the fieldwork, 51 active individuals were observed at two locations: Galeana (5): two males, two females, one unsexed; and Cañon de San Isidro (46): 28 males, 12 females, four unsexed. The most active seasons for the species were spring (37): 22 males, 11 females, four unsexed; and summer (14): seven males, three females, four unsexed.

The majority of the males of this species were observed in the spring and summer, and most of the observed specimens were adults. The activity pattern varied seasonally. During the spring, most of the activity was recorded between 1100–1900 h but remained generally constant throughout the day, whereas in the summer the activity occurred between 1000–1800 h. Similar to other species of lizards, the pattern of activity during the spring seems to be unimodal, whereas during the summer it tends to be bimodal with peaks of activity in both morning and afternoon (Fig. 2). In general, more activity was observed after periods of rain.

Individuals were located in cool, moist, and shaded microhabitats, mainly on rocks (65%), leaf litter (16%), vegetation (11%), and soil (8%) (Fig. 3). In general, they seemed to avoid direct exposure to sunlight. It is likely that abiotic factors (such as temperature and humidity) are the most important factors that influence the activity patterns and microhabitat selection (Angert et al. 2002; Pal et al. 2010). This could explain why the modeling of the ecological niche indicated that bioclimatic isothermality was the variable that influenced the distribution *G. parvus* in the localities within the Sierra Madre Oriental.

Table 1. Body temperature (T_a) , air temperature (T_a) , and substrate temperature (T_s) for *Gerrhonotus parvus* in Sierra Madre Oriental, Nuevo León.

	Season	N	Mean	SE	Minimum	Maximum
Body temperature (T _b)	Spring Summer	37 14	24.50 25.59	0.58 1.38	17.80 13.40	30.10 32.40
	Total	51	24.80	0.56	13.40	32.40
Air temperature (T_a)	Spring Summer	37 14	23.59 24.77	0.63 1.31	13.80 10.60	32.00 31.60
	Total	51	23.92	0.58	10.60	32.00
Substrate temperature (T_s)	Spring Summer	37 14	21.29 23.81	0.61 1.18	15.00 11.60	29.60 30.20
	Total	51	21.91	0.56	11.60	30.20

These localities fall within the geographic provinces of Gran Sierra Plegada and Sierra y Llanuras Occidentales (Band-Leal 2016).

Temperature Measurements

Temperatures by gender. The body temperature (T_b) averages of adult males $(24.72 \pm 0.79 \, ^{\circ}\text{C}, \, \text{N} = 31)$ and females $(24.10 \pm 1.00 \, ^{\circ}\text{C}, \, \text{N} = 15)$ were not significantly different $(F_{1.43} = 0.21, \, p = 0.64)$.

Temperatures by season. Seasonally, the body temperatures (T_b) obtained from 37 specimens in the spring (average: 24.50 ± 0.58 °C, range: 17.80-30.10 °C), and from 14 specimens in summer (average: 25.59 ± 1.38 °C, range: 13.4-32.4 °C) were not significantly different ($F_{2,49} = 0.66$; p = 0.51, Table 1).

The air temperature (T_a) averages for *G. parvus* sites in the spring for 37 specimens (average: 23.59 ± 0.63 °C; range: 13.80-32.00 °C) and in the summer for 14 specimens (average: 24.74 ± 1.31 °C, range: 10.60-31.60 °C) were not significantly different ($F_{2,49} = 0.84$; p = 0.43, Table 1).

The substrate temperature (T_s) averages for *G. parvus* sites in the spring for 37 specimens (average: 21.29 ± 0.61 °C; range: 15.00-29.60°C) and in the summer for 14 specimens (average: 23.81 ± 1.18 °C; range: 11.60-30.20°C) were not significantly different ($F_{2,49} = 2.52$; p = 0.09, Table 1).

Correlations between the temperatures. The ANOVA results showed differences between T_b , T_s , and T_a ($F_{2,45}$ = 11.27; p = 0.004). Pair-wise comparisons (Tukey Test) showed that the average body temperature was different than the average substrate temperature (q = 4.544, p < 0.05), the average body temperature was not different than the average air temperature (q = 1.08, p > 0.05), and the average air temperature was different than the average substrate temperature (q = 3.46, p < 0.05).

The body temperature presented a positive and significant relationship with T_a ($R^2 = 0.29$, p < 0.05; $T_b = 0.55T_a + 12.52$) and with T_s ($R^2 = 0.52$, p < 0.05; $T_b = 0.68T_s + 8.07$) (see Fig. 4). The slope value for

the regression of the body temperature (T_b) and air temperature (T_a) was 0.55, and for the regression of the body temperature (T_b) and substrate temperature (T_s) it was 0.68.

Discussion

The body temperatures recorded for active males and females of G. parvus (24.72 \pm 0.79 °C and 24.10 \pm 1.00 °C, respectively) are within the range of the optimum thermal gradient for individuals of the genus Gerrhonotus, which ranges from 21 to 32 °C (http://madisonherps.org/guwp/wp-content/uploads/2016/07/AlligatorLizards.pdf).

The lack of a significant difference between the body temperatures (T_b) of females and males of G. parvus (Fig. 5) was also observed by Fierro-Estrada (2013) for Abronia taeniata. This feature may be due to the fact that the two sexes occupy very similar microhabitats. In another species of the same genus (Gerrhonotus infernalis), Garcia-Bastida (2013) observed male-female couples sharing the same place of refuge for several weeks, which might be the same situation for G. parvus. On the other hand, G. infernalis has an average body temperature of 22.9 °C in spring and summer (Garcia-Bastida 2013). This species tends to occur in more shaded microhabits

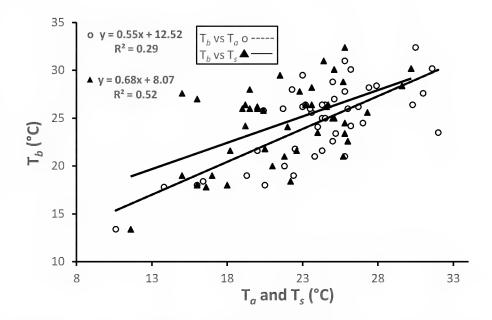


Fig. 4. Relationship between body temperature (T_b) , air temperature (T_a) and substrate temperature (T_s) for *Gerrhonotus parvus* of Sierra Madre Oriental in Nuevo León, Mexico.



Fig. 5. Specimens of (A) male Gerrhonotus parvus and (B) female Gerrhonotus parvus.

Table 2. Average body temperature (T_b) and relationships of body temperature with substrate temperature (T_a) and air temperature (T_a) in several species of Anguidae. An asterisk (*) indicates body temperature was taken in the shade.

Species	Average T _b (°C)	Range T _b	R^2 of T_b vs. T_s	R^2 of T_b vs. T_a	References	Thermoregulatory trends
Barisia imbricata	26.6 22.4	12–34 11–30	0.43 0.18	0.30 0.20	Lemos-Espinal et al. 1998 Muñoz-Brito 2013	Thigmothermic, eurythermic
Abronia taeniata	22.3	14–30	0.73	0.76	Fierro-Estrada 2013	Thermoconforming Facultative eurythermic
Gerrhonotus infernalis	20.7	18–34	0.98	0.83	García-Bastida 2013	Thermoconforming Thigmothermic, eurythermic
Elgaria paucicarinata	25.4	20–31	0.84	0.80	Valdez-Villavicencio and Galina- Tessaro 2014	Thermoconforming Thigmothermic
Gerrhonotus parvus	25.0	13–32	0.52	0.29	This study	Thermoconforming Thigmothermic, eurythermic

than G. parvus to avoid direct contact with the sun's rays, and it occupies much higher rocky microhabitats that are more exposed to the sun when it is active. Differences in the average body temperatures measured for these two species are perhaps due to the differences in the weather conditions and the elevations of the areas where they occur. Gerrhonotus parvus inhabits a variety of plant communities in arid mountainous areas, such as pine-oak forest, pine forest, and oak forest in transition (http://www.fcb.uanl.mx/herpetologia); and is more commonly found at 1,600–1,650 m (Canseco-Márquez and Mendoza-Quijano 2007) and especially among rocks and within leaf litter. In contrast, G. infernalis is most abundant at elevations of 1,360–3,400 m, usually occupying rock crevice microhabitats, and is distributed from semi-desert regions to rocky pine forests (Good 1988; Lemos-Espinal et al. 2018). As in G. infernalis, there is an increase in the activity of G. parvus in the spring and summer months after the rains.

With respect to its trends as a thermoregulator, two pieces of evidence might indicate a passive temperature thermoconformism in G. parvus. The first is that the slope of the regression for T_b vs. $T_a(0.55)$ was less than the slope for T_b vs. T_s (0.68). Based on the criteria proposed by Huey and Slatkin (1976), this species presents a trend toward the passive thermoregulator strategy (Garcia-Rico et al. 2015). Being a thermoconforming lizard has certain implications. For example, when not exposed to the sun, it becomes less conspicuous to potential predators (Huey and Slatkin 1976). On the other hand, having lower body temperatures than other lizards, as do many of the members of the genus Sceloporus, gives them the benefit of losing less water to evaporation (Hertz 1992). We can also assume that the trend of G. parvus and other species of anguids (Barisia imbricata, Abronia taeniata, Gerrhonotus infernalis, and Elgaria paucicarinata) to show activity at low temperatures (Table 2) is an adaptive strategy that allows them to make the best use of the resources in the habitat, with less competition for food and space.

The second piece of evidence that might indicate passive thermoregulation, according to the criteria of Huey and Slatkin (1976), is that this species has a low correlation for T_b vs. T_a ($R^2 = 0.29$), which is lower than that for T_b vs. T_s ($R^2 = 0.52$). This pattern suggests that G. parvus is thigmothermic and depends more on the temperature of the substrate (T_s) than the temperature of the air (T_a) to passively regulate its body temperature (T_a) . In this way, it obtains its heat by using thermoconformity and a thigmothermic process, which is consistent with the patterns presented by other species of anguids, such as Abronia taeniata (Fierro-Estrada 2013), Elgaria paucicarinata (Valdez-Villavicencio and Galina-Tessaro 2014), and Gerrhonotus infernalis (García-Bastida 2013). Likewise, the members of the related family Xenosauridae and its single genus *Xenosaurus* also tend to be thermoconforming and thigmothermic species due

to their extremely secretive habits (Woolrich-Piña et al. 2012).

Other authors have found relationships between ambient temperatures and the body temperature in other species of the family Anguidae, such as *Gerrhonotus multicarinatus* (Cunningham 1966) and *Mesaspis monticola* (Vial 1975). Lemos-Espinal et al. (1998), however, found no correlation between ambient temperatures and body temperatures of *Barisia imbricata*.

We must highlight that in this study we found active specimens of G. parvus at 13.4 °C, which coincides with data recorded by Fierro-Estrada (2013) for Abronia taeniata and those published for other species in family Anguidae. According to Fierro-Estrada (2013), activity at such low temperatures in the family Anguidae suggests that these species possess certain physiological characteristics which allow them to be active at temperatures below the average T_b of many lizards.

Conclusions

Gerrhonotus parvus and the majority of anguid species that are thermoconformers tend to change their body temperature as the environmental temperature of their refuge changes, or with some degree of exposure to the environment. Likewise, this species and the majority of members of the family Anguidae are thigmothermic, and can passively capture heat by conduction from the surface with which they are in contact. Finally, we must consider that the wide range of body temperatures of this lizard and many other anguids gives them the possibility of exhibiting eurythermy, so they will probably respond adequately to the consequences of climate change. In fact, predictive models have determined that the Anguidae family is least vulnerable to the effects of global warming (Sinervo et al. 2010).

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